06-08

Final Report to the **Western National Parks Association**:

Reproductive and Physiological Fitness in Rare and Common *Dudleya* Species

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INTRODUCTION

Goals

Overall the goal was to investigate various aspects of *Dudleya* species' habitat specificity, life histories, physiology, and growth in order to compare taxa for these factors, possibly finding reasons for the differences in their rarity. Specifically: (1) *Dudleya* taxa grow in microclimates with particular environmental conditions. In order to ascertain the importance of these conditions habitat variables were measured at the sites where the different taxa occurred. (2) The species were compared by several life-history variables such as time to first reproduction, reproductive output, and size in the wild. (3) Plants were subjected to one of three watering treatments – no added water, misting during the heat of the day, or watering the roots – and then photosynthetic yield and growth were monitored to see how the plants responded physiologically to water stress. (4) Gardens were established at a coastal site and at an inland site to test the hypothesis that plants in the coastal garden will grow larger or have greater survival percentages than plants grown in the inland garden and that these differences will be greater for rare species than for common species. (5) Plants were grown in cracks between bricks to compare the root:shoot ratios. Since these plants grow in low water environments, differences in energy allocations to roots versus shoots could affect stress tolerance.

Study taxa and the status of each

There are nine taxa of *Dudleya* that grow in the Santa Monica Mountains. They are perennial succulents that grow on rock outcrops in cracks, often amid mosses, in shallow soil deposits on rocks, and rocky soils (Moran 1951, Bartel 1993, McAuley 1996, Reifner et al. 2003). The study region has a Mediterranean climate with mild wet winters and hot dry summers. Their growing season starts with winter rains and extends through the spring. Inflorescences can start to form as early as December. The season of blooming varies by species. Over the summer, they become dormant: inflorescences dry out and in some species break off, the leaves of the rosette close, and the outer-most leaves become dry but remain intact. *Dudleya parva* and *D. blochmaniae blochmaniae* are exceptions in that their shoots are vernal; thus they die back to underground structures during the summer. In general, *Dudleya* fruits ripen over the summer. Seeds are dispersed starting in late summer when the follicles become dry and open. Seed germination is activated by rain (or persistent moisture). After consistent rains, the rosettes open revealing the living inner leaves and growth resumes. For the species with vernal leaves new growth springs up from underground structures (pers. obs.).

Currently there is no conservation or recovery plan for the threatened taxa occurring in the Santa Monica Mountains (USFWS 1999). As such there is a serious need to know the ways in which each rare taxon is or is not autecologically distinct.

Several of the local taxa have protected status, whereas three are quite common at many sites:

D. cymosa marcescens	Federally listed as threatened, State listed as rare
D. blochmaniae blochmaniae	Rare, not listed
D. parva	Federally listed as threatened
D. cymosa ovatifolia	Federally listed as threatened
D. verityi	Federally listed as threatened
D. cymosa agourensis	Federally listed as threatened
D. caespitosa	Common
D. lanceolata	Common
D. pulverulenta pulverulenta	Common

METHODS

Characterizing taxa in the wild and growing families of seedlings

Twelve sites, with 1 to 3 *Dudleya* species per site, were included in the initial survey. The study region included the Santa Monica Mountains and surrounding areas in parts of two counties. Sites in Los Angeles County were Malibu Creek State Park (34.103° N, 118.734° W), Cornell Corners (34.110° N, 118.775° W), Semler Open Space (34.146° N, 118.806° W), and Seminole Hot Springs (34.107° N, 118.791° W). Sites in Ventura County were Joel McCrea Wildlife Preserve (34.236° N, 118.859° W), Wildwood Regional Park (34.219° N, 118.919° W), Rancho Potrero Open Space (34.167° N, 118.946° W), Thornhill Broome Beach (34.084° N, 119.036° W), Leo Carrillo State Park (34.046° N, 118.928° W), Conejo Mountain (34.188° N, 118.984° W), and California State University, Channel Islands (34.162° N, 119.043° W).

Fruits were collected from mid-July through the end of August. Three fruits each were collected from 30 individuals, from 2 or 3 populations of each species. At the time of fruit collection, data on the parent plant's number of inflorescences, tallest inflorescence height, number of fruits, rosette diameter, longest leaf length, number of leaves, and the distance of the five closest neighbors of the same species were recorded.

In December 2005, seeds for all nine taxa were sown. Pots were kept in flats in a greenhouse. Numbers of sprouted seedlings were counted. Seedlings were transplanted between February and April 2006, once most or all of the individuals in a pot had 2 to 3 post-cotyledonous leaves.

Watering treatments

Three watering groups were established followed by measurements of photosynthesis and growth. The plants were located on the California State University, Northridge campus (CSUN: 34.239° N, 118.531° W). The **water group** was watered weekly unless it rained that week. The **mist group** was misted every 15 minutes during the 4 warmest hours of the day. The **no water group** received natural precipitation only, of which there was none for about the first 6 months. The treatments were started in early June.

Photosynthetic activity was determined by using a PAM Fluorometer (PAM-2000, Walz, Effeltrich, Germany). Six readings were taken per plant: the upper and middle part of an outer, middle, and inner leaf. The maximum of the six readings was used in the analyses reported here. Readings were of effective quantum yield (not dark-adapted). Readings were taken from August 2006 to February 2007. The presence of inflorescences was also recorded.

Field Gardens

Two gardens were planted out in different environments, **inland** and **coastal**, within the naturally occurring range of the common species. The coastal garden site was in Zuma Canyon (34.106° N, 118.819° W). The inland garden site was in the mountains between Woodland Hills and Calabasas (34.118° N, 118.585° W). Plants were planted out in June 2006. Plants were watered weekly for 4 weeks to allow them to become established in the gardens. After that point they received only natural precipitation, which was very limited for several months after garden establishment. Every two months, from June 2006 to June 2007, data were collected on the number of leaves, longest leaf length, and number of inflorescences of each individual. Final size and reproductive data were collected in November 2007.

Brick Wall

All nine taxa were grown in a common garden between clay bricks (a thin layer of soil was placed between the bricks) in order to simulate the natural growth of roots in cracks between rocks. The brick wall was constructed in July 2006 at the CSUN campus.

Plants were watered after transplantation and from November 2006 to July 2007. From July 2006 to September 2007, every two months, data on the number of leaves, longest leaf length, and number of inflorescences of each individual were recorded. Plants were removed between September and November 2007. Roots and rosettes were dried and weighed to find biomass dry weights.

RESULTS

Characters of the Species

Table 1 lists habitat characteristics for the study taxa. The average distance of the five closest neighbors (a measure of population density) ranged from 6.3 to 501.4 cm. In general, rare taxa tended to have denser populations than did common taxa (p = 0.04, n = 9). Slope of the substrate a given individual was growing on ranged from flat (0°) to vertical (90°). There were no significant differences between rare and common taxa. Rare taxa tended to grow on substrates with aspects within 90° of north, whereas common taxa grew on substrates with aspects greater than 90° from north (p = 0.008, n = 9). Most taxa tended to be shaded only by the rock outcrops on which they grew, but inland taxa (especially *D. cymosa marcescens* and *D. cymosa ovatifolia*) could also be shaded by trees.

Table 2 gives some growth and life history characters for each of the nine taxa. Longest leaf length ranged from 1.4 cm to 11.7 cm. The leaves of common taxa tended to be longer than those of rare taxa (p = 0.009, n = 7). Number of leaves ranged from 5 to 44. *Dudleya pulverulenta pulverulenta*, a common species, had the greatest number of leaves but differences between rare and common taxa were not significant. Inflorescences were between 11 cm and 88 cm tall, and a trend was seen with common taxa having taller inflorescences than rare taxa (p = 0.00024, n = 9). Number of fruits per individual ranged from 10 to 157. Rare taxa tended to produce fewer fruits per individual than common taxa did (p = 0.008, n = 9). Numbers of seeds per fruit, from 17 to 551, were greater for common taxa than for rare taxa (p = 0.026, n = 9). Additionally, plants that produced more fruits also produced more seeds per fruit ($p < 0.05$, r = 0.712, n = 9). Percent of seeds that germinated ranged from 43% to 80% and percent that survived to be transplanted ranged from 81% to 96%. There was no clear trend in germination or survival percentages between rare and common taxa ($p > 0.05$, r = 0.662, n = 9). In general, number of reproductive individuals increased from the first to the second spring except for two taxa, *D. blochmaniae blochmaniae* and *D. parva*, the two with vernal leaves. Rare taxa had a greater number of individuals reproduce in their first and second springs than common taxa did.

Watering Treatments

Figures 1-2 show the maximum photosynthetic yields for each species in August and December. The mist group tended to have much higher yield readings than the water or the no-water groups during the hot season; and the differences between water versus no-water were relatively small and varied by taxon. By December, after it had rained, the no water group had the highest yields followed by the mist and water groups. This trend was consistent across all taxa. Differences in yields between the treatments were slight and varied by taxon.

Field Gardens

Leaf length and number of leaves were greater for all taxa growing at the coastal site than at the inland site. Figures 3-11 show how size, the logarithm of the length of the longest leaf times the number of leaves, differed between coastal and inland sites for the nine taxa. The area between the lines on the graphs indicates how much a species diverged between the two sites. Rare species such as *D. cymosa marcescens* displayed a larger disparity during the dry season than common species such as *D. caespitosa.*

Brick Wall

Figure 12 shows the correlation of root plus shoot biomass dry weights and root to shoot ratios. Root plus shoot biomass dry weights clustered into five groups. Rare taxa occupied the first three groups with lower weights and common taxa the remaining 2 groups with heavier weights. Most of the taxa generally had similar root to shoot ratios except for *D. pulverulenta pulverulenta* that differed from all of the other taxa.

Figure 13 shows the correlation of root to shoot ratios to maximum differences in size (as measured by the product of leaf length and number of leaves) between plants growing in the inland garden and those in the coastal garden. Rare taxa, those with the smallest root plus shoot dry biomass weights, had the greatest differences in size.

SIGNIFICANCE OF STUDY

Conclusions

Before this study, one might have jumped to the conclusion that some of the varieties were merely different in characters of little biological importance, like differences in flower color. Actually, they are distinct in many features of where and how they grow and reproduce that are not obvious to the casual observer.

Dudleya taxa tend to grow in areas where there are few other plants (pers. obs.), limiting their competition for nutrients, water, etc. The denser populations of the rare taxa subject them to competitive stress which may result in greater adult mortality for the rare taxa not experienced by the more sparsely spaced common taxa.

The habitats where rare and common taxa grow are similar in that they are on rocks or in rocky soil (Moran 1951, Bartel 1993, McAuley 1996, Reifner et al. 2003), but there are microclimate differences between sites where rare and common taxa grow. Rare taxa require substrates that face close to north or, if they are inland, that are shaded by trees. These requirements limit the places where these taxa can occur, contributing to their rarity.

Common taxa tend to be larger bodied than rare taxa as evidenced by the differences in leaf length, leaf number, and dry biomass weight. This size difference can be explained by differences in environment and energy allocation. Coastal plants, living in a cooler moister environment, may have greater photosynthetic activity leading to greater growth in size than inland plants, growing under harsher environmental conditions. The inland plants were smaller in size most if not all of the time they were in place. This size difference was greater in rare taxa.

Common species delay reproduction for at least one spring, allocating their energy to growth instead, allowing them to attain a greater size than rare plants do. Conversely, rare species allocate their energy to reproduction their first spring and remain small. One possible consequence of energy allocation at a young age to growth is greater survival, because a larger plant can acquire and store more energy, nutrients, and water than a small plant can.

Another consequence of larger body size is greater energy output for reproduction when they do eventually bloom (Pitelka 1977, Metcalf et al. 2006). Common plants produced more fruits, a greater number of seeds per fruit, and taller inflorescences than smaller rare plants. Having greater reproductive output allows for a greater possibility of seeds germinating and becoming established in a population, leading to greater population size and/or stability. Furthermore, having a taller inflorescence can increase seed dispersal distance (Lloyd et al. 2003), increasing the likelihood of establishment of individuals at another suitable location.

<u>Products</u>

In addition to this report other products resulting from the funding are or will be:

1. A paper in the book "Flora and ecology of the Santa Monica Mountains: Proceedings of the 32nd annual Southern California Botanists symposium" (special publication #4) and an accompanying presentation given to the Southern California Botanists Society.
2. Presentations given to the California Botanical Society (February 2007), the Ecological Society of America (August 2007) and Botanical Society of America (July 2008).
3. A master's thesis and degree in Biology from California State University, Northridge
4. A publication to be submitted to a national scientific journal. This paper will be a much more statistical treatment of the results than presented in this report.

<u>Park management and resource interpretation</u>

This is the first study to systematically examine the life history patterns and ecological requirements of the rare endemic federally listed threatened *Dudleya* species of the Santa Monica Mountains. It was developed after discussion with park resource management staff and is designed to provide the baseline information necessary for development of the park's mandated long-term monitoring and conservation/recovery programs for these species. This study also provides scientific information needed to allow the park to effectively comment on development proposals for private land in the Recreation Area that can impact the *Dudleya* species prioritized for conservation.

Furthermore, this study provides interpretive and educational information on species that the park has prioritized for protection and management. Park staff report that the public finds *Dudleya* to be curious and attractive. As such, these species may be used to develop both field and school programs on important park conservation concepts such as rare and endemic species, the meaning of habitat and habitat specificity, and plant adaptations to their environment, The park is using the information from this study to create a double-page flyer on *Dudleya* species to be distributed at the visitor center and during relevant park functions.

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Table 1. Population density and habitat characteristics of *Dudleya* taxa growing in the Santa Monica Mountains.

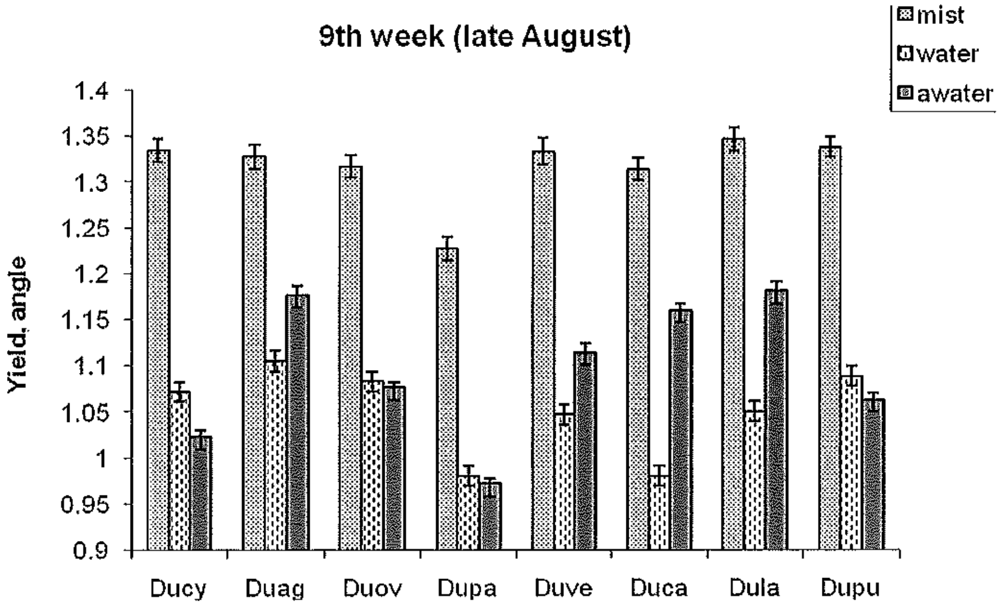
	Nearest neighbor distance	Slope	Aspect	Shade
*Dudleya cymosa marcescens**	6.6 cm	55-90°	30° & 350°	By trees
*Dudleya blochmaniae blochmaniae**	7.4 cm	0-40°, most 20°	30-0-310°	Only by rock outcrops
*Dudleya parva**	10.8 cm	0-90°, most 10°	20–0-300° most w/in 10° of N	Only by rock outcrops
*Dudleya cymosa ovatifolia**	25.8 cm	10-90°, most >50°	0-180°	By trees or far side of canyon
*Dudleya verityi**	6.3 cm	10-90°	55° - 0° - 270°	Only by rock outcrops
*Dudleya cymosa agourensis**	68.3 cm	25-90°	90-0-340°	Only by rock outcrops
Dudleya caespitosa	50.8 cm	0-90°, most 90°	230-0-320°	Only by rock outcrops
Dudleya lanceolata	168 cm	0-90°	50-0-140°	Variable
Dudleya pulverulenta pulverulenta	501.4 cm	0-90° 1/3 at 90°	20-0-340°	Variable

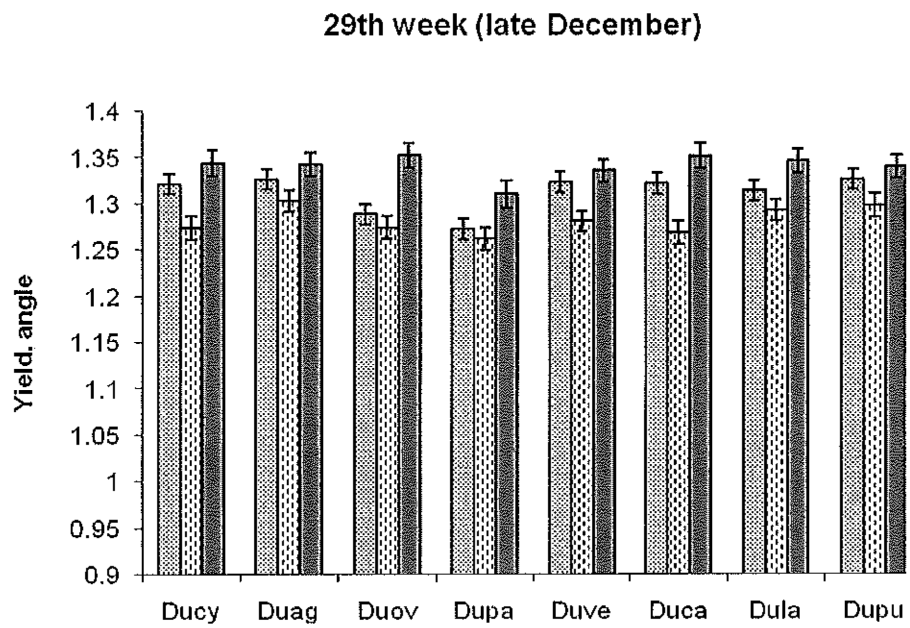
Asterisk indicates rare taxon. Data were collected from sites in the Santa Monica Mountains Region over the summer of 2005. Plants were chosen from two or three populations for each taxon. Nearest neighbor distance, distance of the five nearest neighbors to the focal plant of the same species, averaged ($n = 30$). Ranges of slope of substrate plant was growing on ($n = 30$), Range of aspects for plants ($n = 30$), List of sources of shade ($n = 30$).

Table 2. Size, reproductive biology characteristics, and reproduction percentages for *Dudleya* taxa in the Santa Monica Mountains.

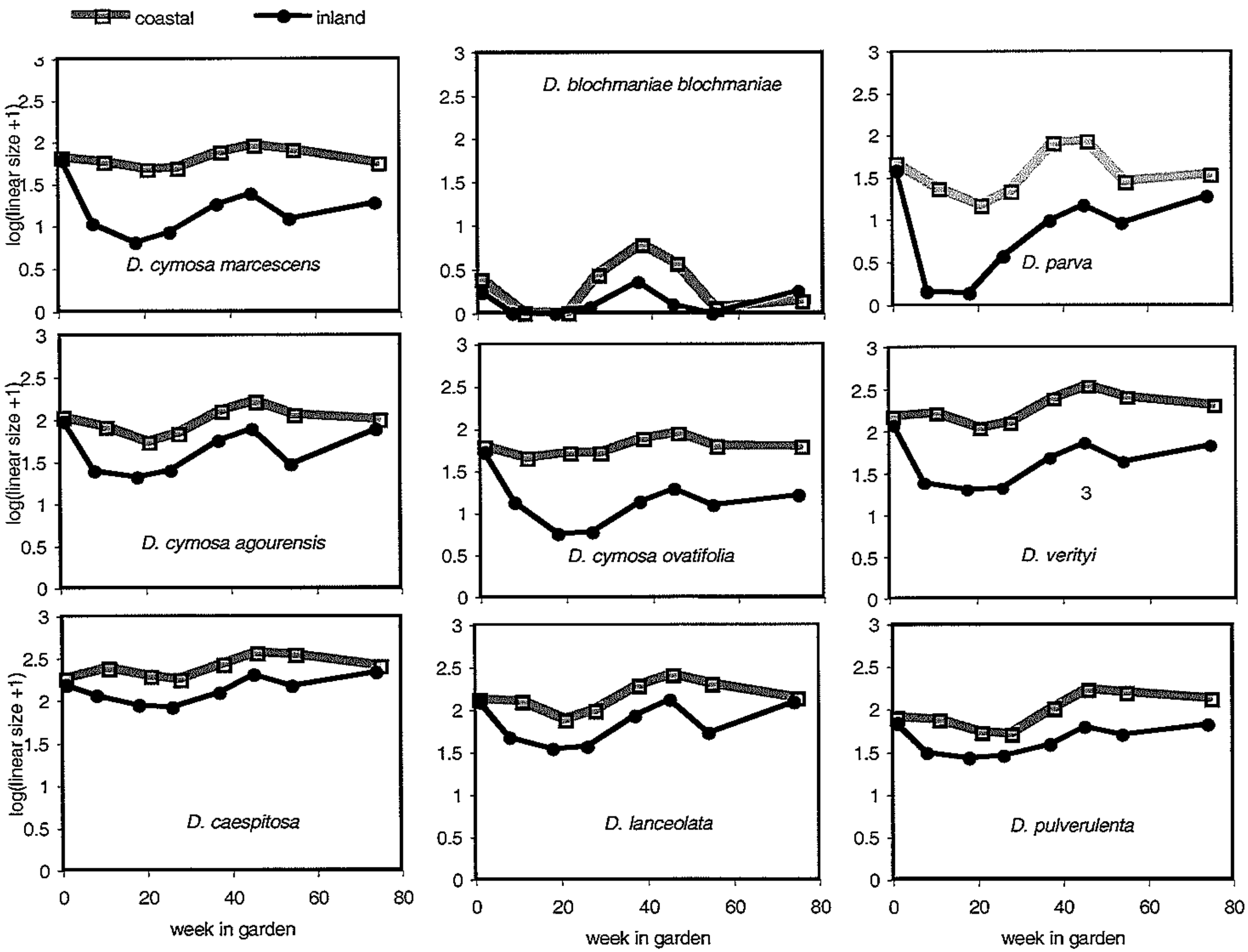
	Longest leaf length	# Leaves	Inflorescence height	# Fruits	Seeds per fruit	% Germination	% Survival	% Reproductive 1st spring	% Reproductive 2nd spring
*Dudleya cymosa marcescens**	1.4 cm	5	11 cm	10	41	43%	86%	76%	98%
*Dudleya blochmaniae blochmaniae**	N/A	N/A	11 cm	29	17	74%	87%	98%	96%
*Dudleya parva**	N/A	N/A	13 cm	24	36	77%	94%	100%	91%
*Dudleya cymosa ovatifolia**	1.8 cm	5	11 cm	19	52	59%	81%	53%	97%
*Dudleya verityi**	1.6 cm	8	12 cm	39	36	60%	87%	95%	99%
*Dudleya cymosa agourensis**	2.6 cm	10	26 cm	74	62	64%	92%	57%	98%
Dudleya caespitosa	6.4 cm	16	49 cm	88	58	73%	94%	0%	53%
Dudleya lanceolata	3.8 cm	7	69 cm	83	123	80%	96%	10%	91%
Dudleya pulverulenta pulverulenta	11.7 cm	44	88 cm	167	551	63%	81%	0%	0%

Asterisk indicates rare taxon. Data and seeds were collected from two or three populations of each taxon in the Santa Monica Mountains Region over the summer of 2005. Plants were chosen from two or three populations for each taxon. *D. parva* and *D. blochmaniae blochmaniae* did not have leaves at the time of data collection. Longest leaf length, averaged (n = 30), Number of leaves, averaged (n = 30), Inflorescence height, height of the tallest inflorescence per plant, averaged (n = 30), Number of fruits per plant, averaged (n = 30). Seeds were sown in December 2005 in 4" pots, 30 seeds per pot in a greenhouse and were fertilized weekly. Seedlings were transplanted between the ages of two to four months, one individual per 4" pot and placed in a shade house. Percentage germinated – maximum number of live seedlings per taxon divided by number of seeds sown. Percentage survival - number of seedlings that survived to be transplanted divided by maximum number of seedlings. Percent reproductive - plants with inflorescences during the first and second spring in each taxon for all experimental groups were totaled and divided by total number of plants per taxon in all groups (separately for each spring).





Figures 1-2. In the heat of August the misting treatment photosynthesized more and watering was not generally beneficial, whereas all treatments photosynthesized similarly in December when it had been cool for some months. (*n* = 30 species per treatment except for *D. cymosa marcescens* 28, *D. cymosa ovatifolia* 28, *D. verityi* 25, *D. lanceolata* 29, *D. pulverulenta pulverulenta* 26). Ducy - *D. cymosa marcescens*, Duag - *D. cymosa agourensis*, Duov - *D. cymosa ovatifolia*, Dupa - *D. parva*, Duve - *D. verityi*, Duca - *D. caespitosa*, Dula - *D. lanceolata*, Dupu - *D. pulverulenta pulverulenta*. *D. blochmaniae blochmaniae* was not included because it has leaves for only part of the year. The maximum yield for each individual was found. Individual maximums were averaged by species. Data were then square root arcsine transformed.



Figures 3-11. Field gardens. *Dudleya cymosa marcescens* (upper left) was one of the smaller-bodied species and had large differences between coastal and inland sites, while *Dudleya caespitosa* (lower left) grew the largest and had about the least difference between coastal and inland sites. (n = 30 species per site except for *D. cymosa marcescens* 26 C, 23 I; *D. blochmaniae blochmaniae* 19 C, 13 I; *D. parva* 26 I; *D. cymosa agourensis* 26 I; *D. cymosa ovatifolia* 26 C, 23 I; *D. verityi* 25 C, 23 I; *D. lanceolata* 29; *D. pulverulenta pulverulenta* 27 C, 26 I). In the graphs size was treated as the logarithm of the length of the longest leaf times the number of leaves. Examining the data for each component measure revealed that both length and number contributed to inland/coastal differences.

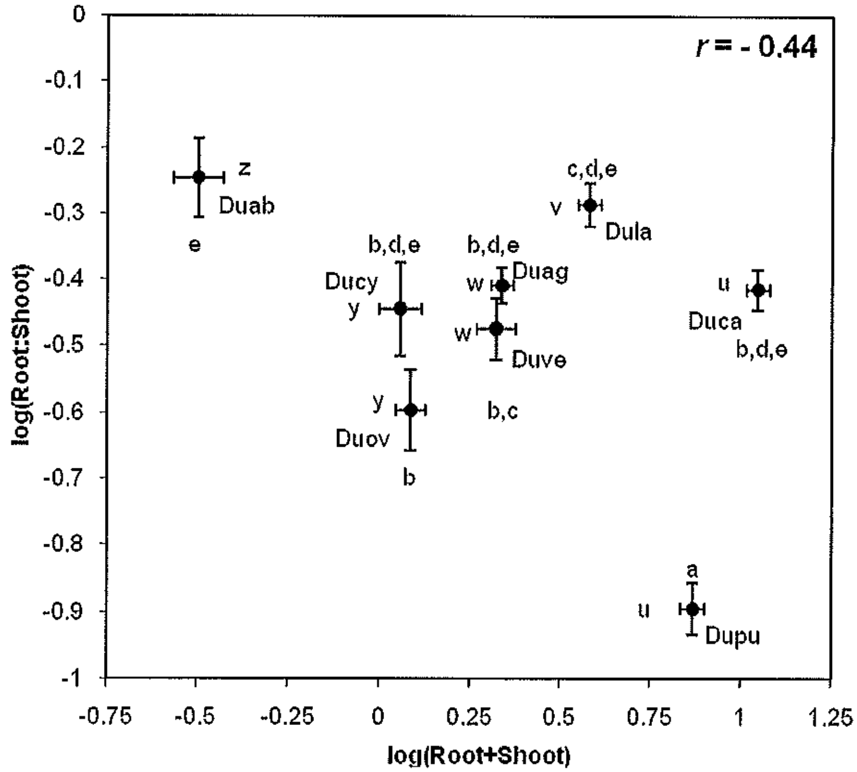


Figure 12. Eight species grown in a brick wall. There was no significant correlation between R:S ratio and total size. Species with a shared letter were not significantly different. Dupa - *D. parva,* Duve - *D. verityi,* Duca - *D. caespitosa,* Dula - *D. lanceolata,* Dupu - *D. pulverulenta pulverulenta. D. blochmaniae blochmaniae* was not included because it has above ground growth for only part of the year.

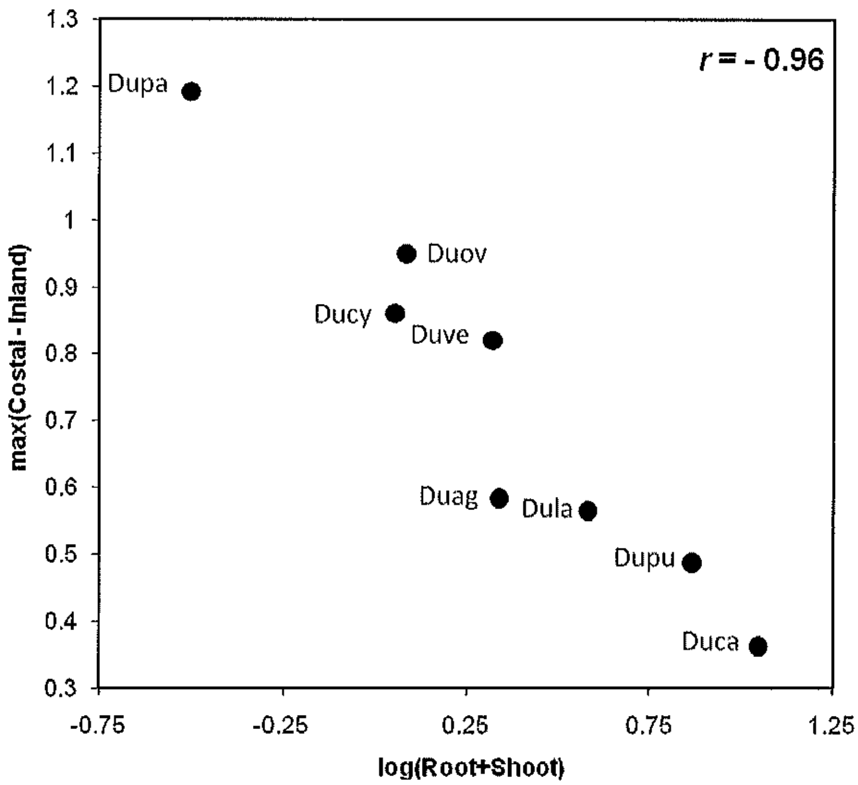


Figure 13. Difference in maximum size of each taxon grown in a coastal garden and in an inland garden correlated with root plus shoot biomass dry weights by taxon. Dupa - *D. parva,* Duve - *D. verityi,* Duca - *D. caespitosa,* Dula - *D. lanceolata,* Dupu - *D. pulverulenta pulverulenta. D. blochmaniae blochmaniae* was not included because it has above ground growth for only part of the year.